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A new theropod dinosaur, represented by a single unusual caudal vertebra, from the Kem Kem Beds (Cretaceous) of Morocco

Abstract - We describe a near-complete distal caudal vertebra from an Upper Cretaceous theropod, discovered in the Kem Kem Beds (Cenomanian) of Tafilalt, Morocco. The specimen exhibits an extremely unusual combination of features, and we herein erect a new species, *Kemkemia auditorei* gen. et sp. nov. The specimen differs from other theropod distal caudal vertebrae in the presence of a relatively inflated neural canal, strongly reduced zygapophyses, a low but very robust neural spine bearing shallow lateral fossae, a mediolaterally concave dorsal surface of the neural spine, and coalescence of the postzygapophyses in a position more proximal than the region where neural spines are absent. Although *Kemkemia* shares some derived features with neoceratosaurs, we provisionally refer it to Neotheropoda *incertae sedis*, pending the discovery of more complete material. Several distal caudal vertebrae from the Maastrichtian of India are similar to *Kemkemia*, and may belong to a closely related taxon.

Key words: *Kemkemia auditorei* gen. et sp. nov., Theropoda, caudal vertebra, Morocco, Cenomanian.

Riassunto - Un nuovo dinosauro teropode, rappresentato da un'inusuale vertebra caudale, proveniente dai Letti del Kem Kem (Cretacico) del Marocco.

In questo studio descriviamo una vertebra caudale quasi completa del Cretacico superiore (Cenomaniano) di Tafilalt, Marocco. Sulla base dell'inusuale combinazione di caratteristiche presenti in questo esemplare, abbiamo eretto una nuova specie di teropode, *Kemkemia auditorei* gen. et sp. nov. Essa si distingue dalle caudali distali dei teropodi noti per: presenza di un canale neurale relativamente espanso, zigapofisi estremamente ridotte, presenza di una spina neurale bassa ma robusta avente deboli fosse laterali, superficie dorsale della spina concava mediolateralmente, fusione delle postzigapofisi che avviene lungo le caudali prossimalmente alla perdita della spina neurale. Sebbene *Kemkemia* condivida alcuni caratteri derivati con i neoceratosauri, attribuiamo provvisoriamente questo taxon a Neotheropoda *incertae sedis*. Numerose caudali distali di teropode del Maastrichtiano dell'India mostrano una morfologia simile a *Kemkemia* e potrebbero dunque appartenere ad un taxon imparentato con il nuovo teropode marocchino.

Parole chiave: *Kemkemia auditorei* gen. et sp. nov., Theropoda, vertebra caudale, Marocco, Cenomaniano.

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Introduction

In recent decades, several theropod dinosaurs have been reported from the mid Cretaceous (Aptian-Turonian) of North Africa (Sereno *et al.*, 1994; Russell, 1996; Sereno *et al.*, 1996; Sereno *et al.*, 1998; Riff *et al.*, 2004; Sereno *et al.*, 2004; Mahler, 2005; Novas *et al.*, 2005a; Brusatte & Sereno, 2007; Sereno & Brusatte, 2008). Most have been referred to abelisauroid and basal (non-coelurosaurian) tetanuran clades of middle to large body size. In May 1999, the Palaeontological Section of the Museo di Storia Naturale di Milano, in collaboration with the Geological Service of Morocco and with the logistical support of F. Escuillié (Eldonia, France) and G. Pasini (Fossilia snc., Italy), carried out a palaeontological expedition in the southern part of the Errachidia Province, Morocco, focussing on invertebrate fauna (Alessandrello & Bracchi, 2003). Prospecting was also carried out in the Tafilalt, near Erfoud. The most interesting find from the region was an almost complete caudal vertebra, collected as a surface find south of Erfoud, a few kilometers to the east of the small village of Taouz and toward the direction of Hamada du Guir (Pasini, pers. comm., 2008; Fig. 1). On the basis of an unusual combination of features present in this vertebra, we formally erect a new species of theropod dinosaur.

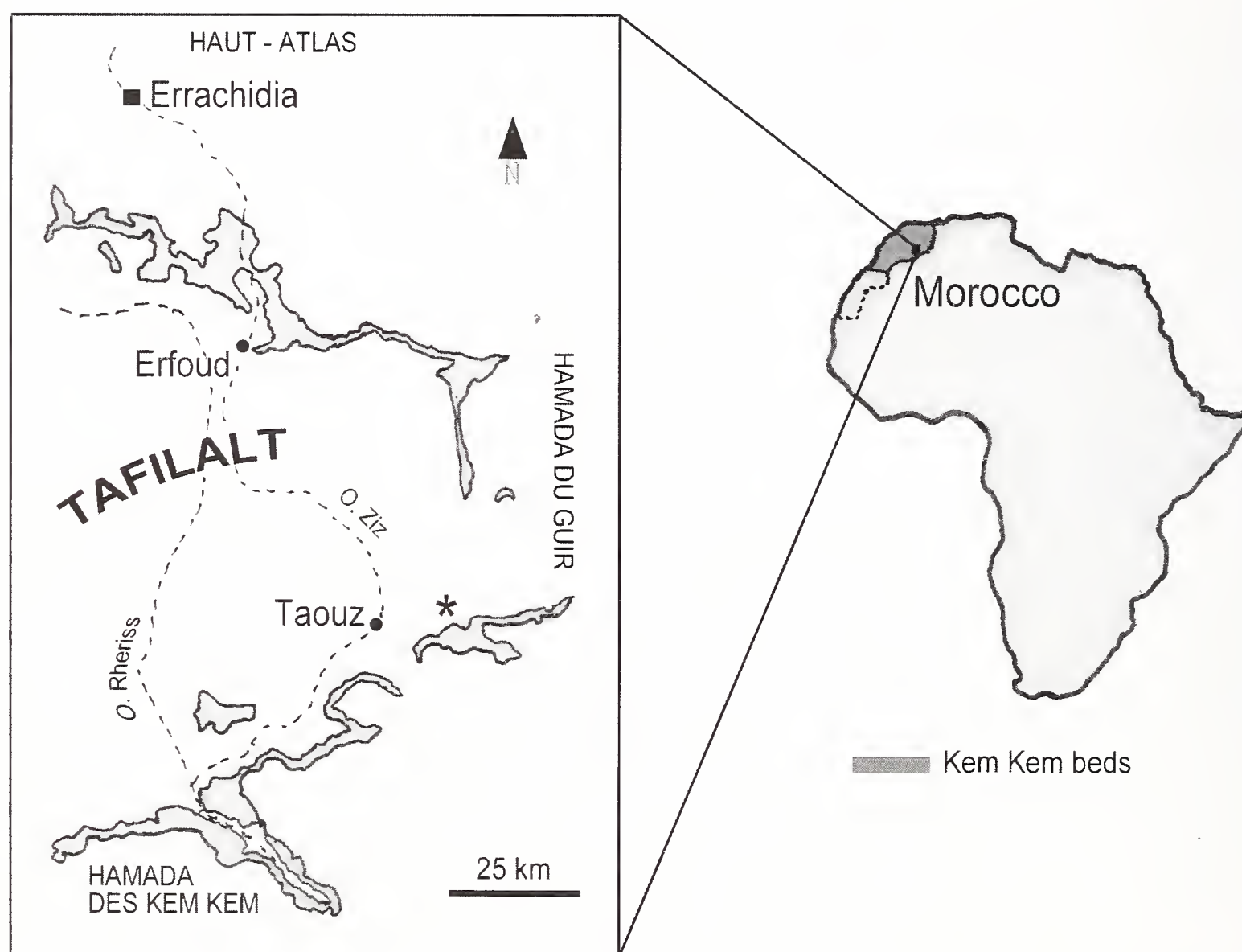


Fig. 1 - Geographic map of the fossil location south of Erfoud, east of the village of Taouz, toward the Hamada du Guir, Errachidia Province, Morocco; the main localities and landscape elements cited in the text are shown in the map. The asterisk marks the site from where the specimen MSNM V6408 was collected (drawing by SM and G. Pasini; based on the original drawing by Garassino *et al.*, 2006).

Fig. 1 - Cartina geografica indicante il punto di rinvenimento dell'esemplare, a S di Erfoud e ad E del villaggio di Taouz, in direzione di Hamada du Guir (provincia di Errachidia, Marocco), in cui sono evidenziati le principali località e i toponimi citati nel testo. L'asterisco indica la località da cui proviene l'esemplare MSNM V6408 (disegno di SM e G. Pasini, basato sul disegno originale di Garassino *et al.*, 2006).

Institutional abbreviations: **GSI:** Geological Survey of India, Kolkata, India; **IGM:** Mongolian Institute of Geology, Mongolian Academy of Science, Ulan Bator, Mongolia; **MSNM:** Museo di Storia Naturale di Milano, Italy; **NMC:** Canadian Museum of Nature, Ottawa, Ontario, Canada; **UCPC:** University of Chicago, Paleontological Collection, Chicago, USA.

Materials and methods

The specimen is catalogued in the Vertebrate Palaeontological Collection of the Museo di Storia Naturale di Milano (MSNM V) as MSNM V6408.

Following Weishampel *et al.* (2004), we adopt the following anatomical terms of the *Nomina Anatomica Veterinaria* (NAV 1994) and the *Nomina Anatomica Avium* (NAA 1993): ventral (toward the belly), dorsal (toward the back), proximal (toward the mass of the body), and distal (away from the mass of the body). For saurischian and ceratosaurian systematic terminologies we follow Padian *et al.*, (1999) and Wilson *et al.* (2003), respectively. Accordingly, we consider Neotheropoda the least inclusive clade containing *Coelophysis bauri* and extant birds; Ceratosauria the most inclusive clade containing *Ceratosaurus nasicornis* but not extant birds; and Tetanurae the most inclusive clade containing extant birds but not *Ceratosaurus nasicornis*.

Systematic Palaeontology

Dinosauria Owen, 1842
 Saurischia Seeley, 1888
 Theropoda Marsh, 1881
 Neotheropoda Bakker, 1986
 ?Ceratosauria Marsh, 1884
Kemkemia auditorei gen. et sp. nov.

Derivatio nominis - The generic name refers to the Kem Kem Beds of Morocco, where the holotype specimen was collected. The specific name honours the Italian palaeoartist Marco Auditore, for his inexhaustible and enthusiastic support of vertebrate palaeontology.

Holotype - MSNM V6408, an almost complete distal caudal vertebra (Fig. 2) of a middle- to large-sized theropod.

Locality - Although GPS data were not recorded, the specimen comes from some kilometers south of Erfoud, east of the village of Taouz, and in the direction of the Hamada du Guir, Errachidia Province, Morocco (Fig. 1).

Horizon - Kem Kem Beds, “Infracénomanien” (Russell, 1996), Cenomanian, Upper Cretaceous (Serenio *et al.*, 1996). The Kem Kem Beds consist of channel-deposited red sandstone (Russell, 1996; Serenio *et al.*, 1996), lithologically identical to the matrix that encrusted the vertebra and filled the neural canal prior to preparation (Pasini, pers. comm., 2008). The specimen was discovered in close association with rostral teeth of the Aptian-Cenomanian elasmobranch *Onchopristis* sp. (Pasini, pers. com., 2008; Rage & Cappetta, 2002; Russell, 1996). The latter is an extremely common find in the Kem Kem Beds and is often found in association with dinosaur remains (Naish, pers. comm., 2009).

Diagnosis - Neotheropod dinosaur bearing distal caudal vertebrae with the following autapomorphies: inflated neural canal, broader than the width of the centrum at mid-length; strongly reduced finger-like prezygapophyses lacking articular facets and failing to reach the level of the articular end of the centrum; robust neural spine (in which the mediolateral width at the apex is at least 30% of the width of the cranial articular surface of the centrum); shallow fossa on the distal half of the lateral surface of the neural spine bounded distally by the postspinal lamina; mediolaterally concave dorsal surface to the neural spine.

Differential diagnosis: *Kemkemia* differs from other theropods, with the possible exception of *Ilokelesia* (Coria & Salgado, 2000) and *Ligabueino* (Bonaparte, 1996), in that the postzygapophyses coalesce at a point in the tail more proximal than the point at which loss of the neural spine occurs.

Description

The specimen MSNM V6408 (Fig. 2; Tab. 1) is a near-complete, well preserved three-dimensional caudal vertebra. The right prezygapophysis is broken at the base; the periosteum along the margins of the proximal and distal articular facets and the articular surfaces for the chevron are missing, although the outline of the chevron facets is still visible (Fig. 2D). The neural arch is completely fused to the centrum and no trace of a neurocentral suture is present. The centrum is amphicoelous, slightly more excavated proximally, and it lacks pneumatic fossae or foramina. A vascular foramen is present on the left lateral surface of the centrum (Fig. 2B). The centrum is elongate, being more than three times longer than it is tall at its proximal end. The proximal and distal articular faces are quadrangular, with a width to height ratio close to 1. The lateral surfaces are dorsoventrally concave, with the right side being slightly more concave than the left. The ventral surface is flat and very narrow, measuring (at mid-length of the centrum) no more than 45% of the ventral width of the articular facets. The neural arch is very elongate, its base occupying almost 90% of the dorsal length of the centrum. The neural canal is rounded and very large, having proximal dorsoventral and mediolateral diameters that are almost 50% the diameters of the proximal articular face of the centrum. Due to the size of the neural canal, the inflated neural arch is visible for almost its entire length when the specimen is examined in ventral view. The left prezygapophysis is an extremely reduced, finger-like process, subtriangular in dorsal view and close to the mid-line, bounding a narrow cleft housing a rounded pit. The proximal tip of the prezygapophysis does not reach the level of the proximal articular face of the centrum and lacks any distinct articular facet. A faint ridge extends from the dorsal mid-line of the prezygapophysis to the proximo-lateral base of the neural spine. This may represent a faint spinoprezygapophyseal lamina. A prominent, sharply defined prespinal lamina is present. It gradually decreases in height toward its proximal end, disappearing at the level of the distal margins of the prezygapophyseal ridges. The prespinal lamina is bounded laterally by two shallow fossae. The distal margin of the neural arch lacks postzygapophyses: it is replaced by a single, small process that does not reach as far distally as the distal end of the centrum. At its proximal end, this process unites with the postspinal lamina. This lamina is less sharp than the prespinal one, but it is

slightly taller, reaching the ventrodiscal margin of the spine table. The neural spine is distally placed and short, being about 20% of the length of the neural arch. In lateral view, the spine is trapezoidal and longer than tall. The spine is broad and robust, having an apical width that is 32% the width of the cranial articular face of the centrum. The laterodistal surfaces of the spine are slightly concave. These concavities are bordered distally by the postspinal lamina. As a consequence, the proximal half of the spine is broader and more robust than the distal one, so the mid-height cross-section of the spine is tear-drop-shaped. The dorsal surface of the spine is ovate, longer than wide in dorsal view and slightly concave in both proximal and distal views. The lateral edges of the dorsal concavity are bounded by slightly developed but clearly defined margins that converge proximally.

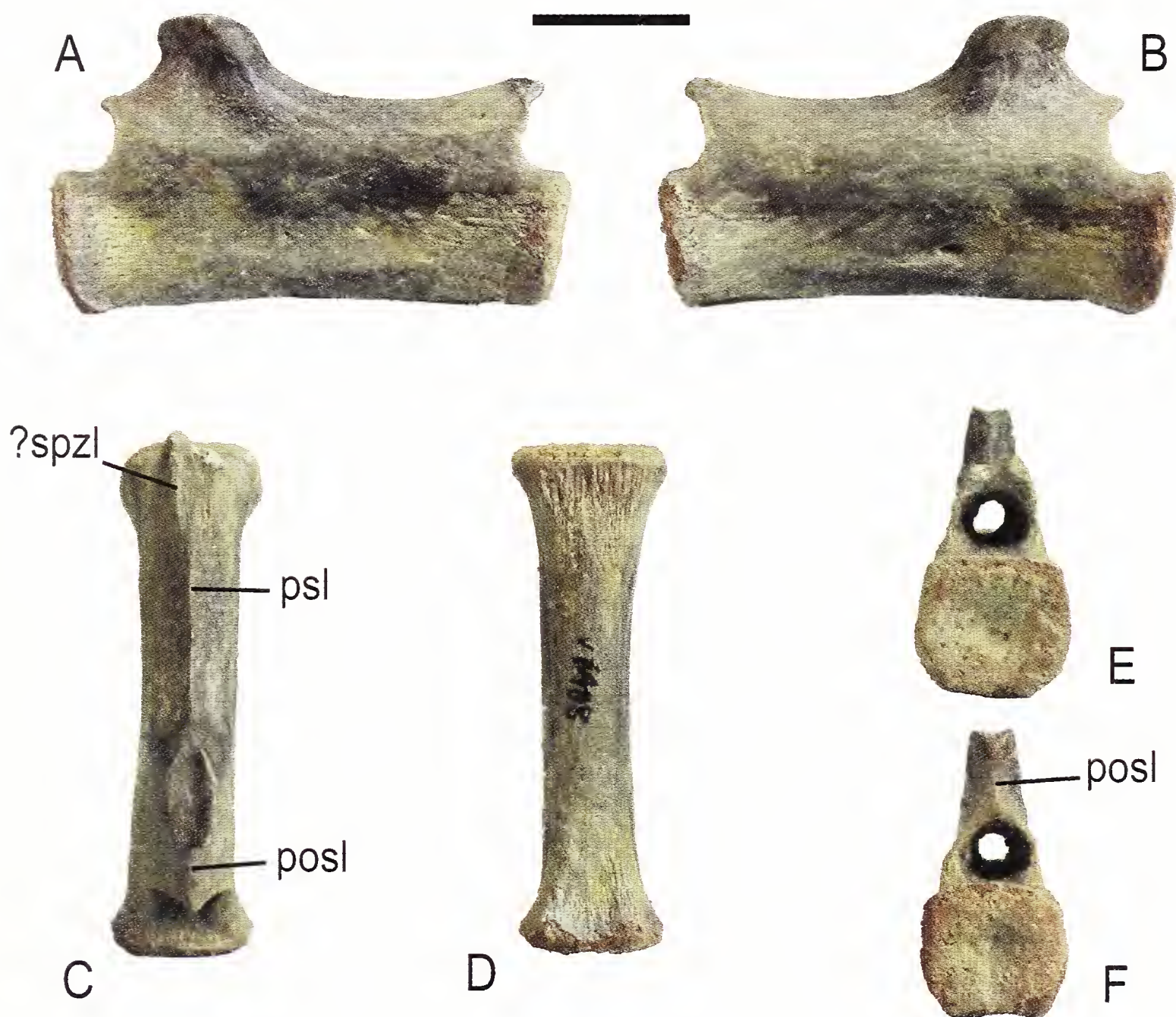


Fig. 2 - Specimen MSNM V6408 in right lateral (A), left lateral (B), dorsal (C), ventral (D), proximal (E), and distal (F) views. Abbreviations: ?spzl, ?spinoprezygapophyseal lamina; psl, prespinal lamina; posl, postspinal lamina. Scale bar equals 2 cm. (Photos by SM).

Fig. 2 - Esemplare MSNM V6408 nelle norme laterale destra (A), laterale sinistra (B), dorsale (C), ventrale (D), prossimale (E) e distale (F). Abbreviazioni: ?spzl, lamina ?spinoprezigapofiseale; psl, lamina prespinale; posl, lamina postspinale. La scala metrica equivale a 2 cm. (Foto di SM).

Tab. 1 - Basic measurements of specimen MSNM V6408.
Tab. 1 - Misure principali dell'esemplare MSNM V6408.

Selected measurements of MSNM V6408	(measurements expressed in mm)
Vertebra: maximum length	60.48
Vertebra: maximum height	33.81
Vertebra: maximum width	17.79
Centrum: maximum length	60.48
Centrum: width at mid-length	7.60
Centrum: proximal facet height	16.53
Centrum: proximal facet width	17.79
Centrum: distal facet height	15.44
Centrum: distal facet width	16.99
Neural arch: maximum height	17.33
Neural arch: length from tip of prz to tip of poz	52.21
Neural arch: width at centrum mid-length	10.91
Neural arch: top of the neural spine length	10.62
Neural arch: top of the neural spine width	5.70

Discussion

Taxonomic affinities and phylogenetic hypotheses of MSNM V6408 - On the basis of the presence of articular facets for the chevrons and the absence of transverse processes, we identify MSNM V6408 as a non-proximal caudal vertebra. The absence of transverse processes combined with the presence of a robust neural spine indicates that MSNM V6408 belongs to the transitional zone between the proximal/middle caudals (bearing both neural spines and transverse processes), and the distal-most vertebrae that lack such structures (Fig. 3). The presence of spinal laminae in caudal neural arches is a derived feature of some saurischian clades (Wilson, 1999): specifically, neosauropods and neotheropods. Accordingly, we compared the vertebra with sauropod distal caudals. MSNM V6408 shares with *Jobaria* and Neosauropoda the presence of prespinal and postspinal laminae (Wilson, 2002). MSNM V6408 shares several features with some neosauropods in which the distal caudals still bear the neural spine. In such taxa, the centrum is elongate (Wilson, 2002; Upchurch *et al.*, 2004), the articular faces are quadrangular (Osborn, 1899, Plate XXVIII; Upchurch *et al.*, 2004), and the ventral surfaces are flattened (Gomani, 1999; Salgado *et al.*, 2004). However, many features present in *Kemkemia* are unusual when compared with sauropod distal caudals: in sauropods the elongate distal caudal centra (having a length to height ratio greater than 3) are often biconvex rather than amphicoelous (Wilson *et al.*, 1999), the base of the neural arch is usually more proximodistally reduced than it is in *Kemkemia*, failing to reach the distal fifth of the centrum; the zygapophyses are more robust dorsoventrally; and the neural spine is more proximodistally elongate and projects distally

beyond the postzygapophyses (Osborn, 1899; Calvo & Salgado, 1995; Gomani, 1999; Salgado *et al.*, 2004; Harris, 2006; Sereno *et al.*, 2007). Moreover, a hypertrophied neural canal has yet to be reported in any sauropod distal caudal vertebra (Osborn, 1899: Plate XXVIII; Osborn & Mook, 1921: Plate LXXII; Gomani, 1999; Salgado *et al.*, 2004), whereas chevron facets and pre- and postspinal laminae do not persist through the distal caudal series in neosauropods (Wilson, 1999; Wilson, 2002; Kellner *et al.*, 2005). In conclusion, while some resemblances are present between MSNM V6408 and the distal caudals of some sauropods, it seems most likely that these similarities are convergent.

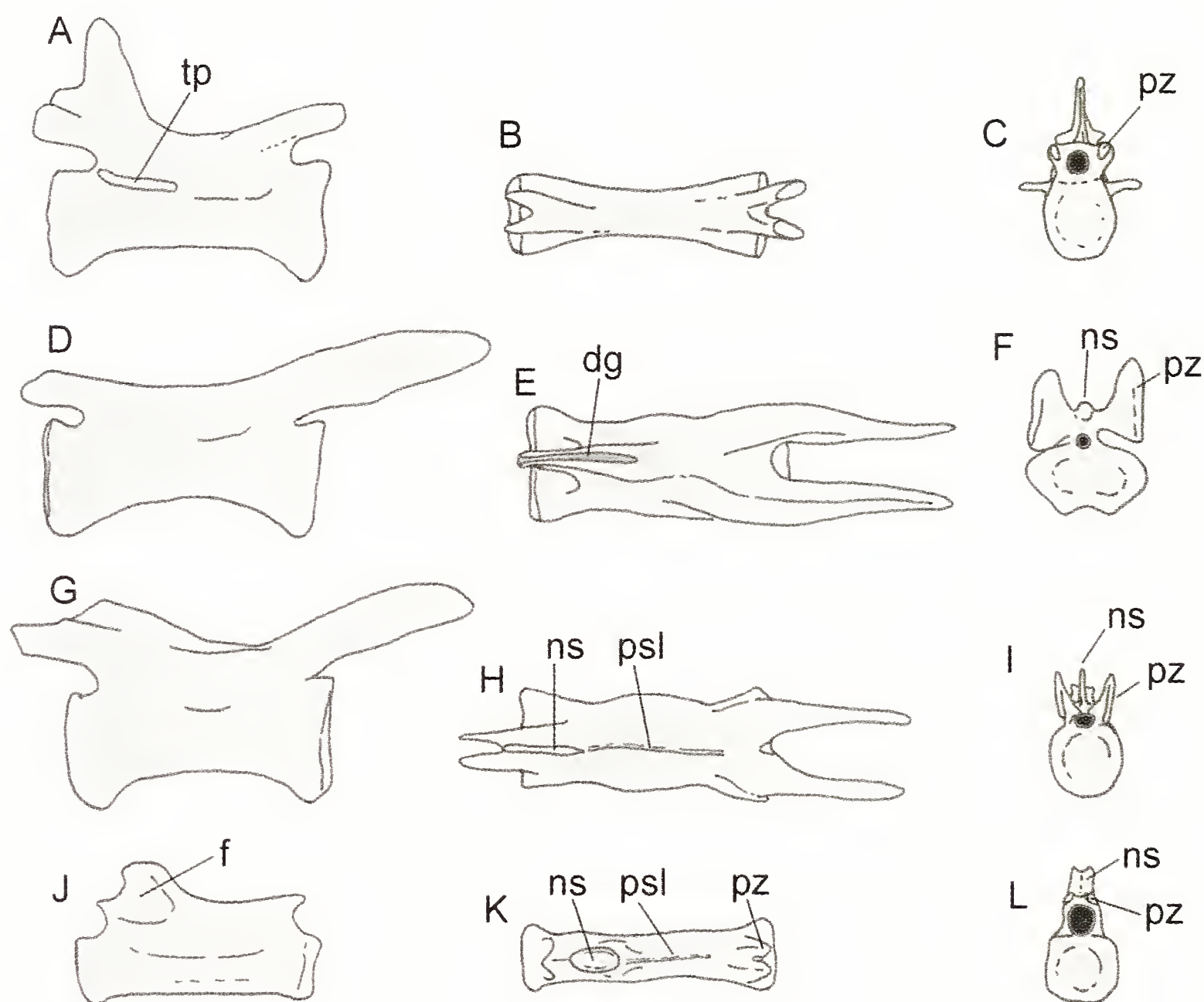


Fig. 3 - Theropod distal caudal vertebrae, in right lateral view (A, D, G, J), dorsal view (B, E, H, K), and proximal view (C, F, I, L): A, C, *Dilophosaurus* (modified from Welles, 1984); B, *Coelophysis* (modified from Colbert, 1989); D, E, *Allosaurus* (modified from Madsen, 1976); F, Ornithomimidae indet. (modified from Longrich, 2008); G-I, *Majungasaurus* (modified from O'Connor, 2007); J-L, MSNM V6408 (this study). Abbreviations: dg, dorsal groove; f, fossa; ns, neural spine; psl, prespinal lamina; pz, prezygapophyses; tp, transverse process. Not shown at the same scale. (Drawing by AC).

Fig. 3 - Vertebre distali di teropodi, nelle norme laterale destra (A, D, G, J), dorsale (B, E, H, K), e prossimale (C, F, I, L): A, C, *Dilophosaurus* (modificato da Welles, 1984); B, *Coelophysis* (modificato da Colbert, 1989); D, E, caudale distale di *Allosaurus* (modificato da Madsen, 1976); F, Ornithomimidae indet. (modificato da Longrich, 2008); G-I, *Majungasaurus* (modificato da O'Connor, 2007); J-L, MSNM V6408 (questo studio). Abbreviazioni: dg, solco dorsale; f, fossa; ns, spina neurale; pz, prezigapofisi; tp, processo trasverso. Non alla stessa scala. (Disegno di AC).

Elongation of the centrum is a widespread feature of theropod distal caudals: it is present in most neotheropods with the exceptions including therizinosauroids more derived than *Falcarius* (Kirkland *et al.*, 2005), oviraptorosaurs more derived than *Protarchaeopteryx* (Senter, 2007), and short-tailed avialians (Chiappe *et al.*, 1999). When compared with other elongate neotheropod caudals, MSNM V6408 shows an unusual combination of features (Fig. 3). The ventral surface is flat and lacks the longitudinal keels and grooves reported in most (Carrano *et al.*, 2002; Rauhut, 2003) - but not all (Osmólska, 1996; Novas, 1997; Kirkland *et al.*, 1998; Barsbold *et al.*, 2000; Carrano *et al.*, 2002; Rauhut, 2003) - theropod caudals. The relatively large size of the neural canal relative to the centrum suggests that this vertebra was not positioned very close to the distal end of the tail (Suzuki *et al.*, 2002; Brochu, 2003).

Size, robustness, and the shape of the neural processes (neural spine, transverse processes and zygapophyses) varies according to the position along the caudal series, and also varies among the different theropod clades.

Neural spine - The neural spine is relatively robust and differs from both the elongate sheet-like spines and the low ridge-like spines present in most theropod middle and distal caudals, being more similar to the robust rod-like middle caudal neural spines of some ceratosaurs (Carrano & Sampson, 2008; Madsen & Welles, 2000; Rauhut, 2003). In particular, the presence of a concave dorsal surface to the neural spine is shared with some mid-caudals of *Ceratosaurus* (Madsen & Welles, 2000). Among neotheropods, the position of the last caudal vertebra bearing a distinct neural spine is variable, and is not necessarily related to the total number of caudal vertebrae. In *Dilophosaurus* the 22nd caudal vertebra is the last one bearing a neural spine (Welles, 1984); in *Allosaurus* it occurs between the 35th and the 38th position (Madsen, 1976); in *Tyrannosaurus* the neural spines reduce after the 13th and the last one is at the 27th position (Brochu, 2003); in *Harpymimus* (Kobayashi, 2004) and *Nomingia* (Barsbold *et al.*, 2000) the neural spines become low crests after the 15th position; in *Sinosauropteryx*, which has the highest known number of caudals (Rauhut, 2003), the neural spines reduce after the 10th position and disappear at the 18th (Currie & Chen, 2001); whereas in paravians there are usually no more than 9 proximal caudals bearing distinct neural spines (Ostrom, 1969; Forster *et al.*, 1998; Mayr *et al.*, 2007).

Transverse processes - The absence of transverse processes shows that MSNM V6408 must have come from the part of the tail distal to the transition point (Russell, 1972; Gauthier, 1986; Tykoski, 2005). The position of the transition point is variable along theropod tails: it is, for example, more proximally located in those taxa closest to birds (Gatesy, 1990). Therefore, the proximal-most position possible for MSNM V6408, based on the absence of transverse processes, varies according to whichever clade it is compared with. In non-tetanuran theropods (Gilmore, 1920) the transition point occurs after the 30th position; in non-coelurosaurian tetanurans (Gilmore, 1920; Madsen, 1976) it occurs after the 25th position; in most coelurosaurs (with the exception of oviraptorosaurs, Barsbold *et al.*, 2000) it occurs at the 12-17th position (Russell, 1972); while in basal paravians it occurs more proximally (Gatesy, 1990; Rauhut, 2003; Turner *et al.*, 2007).

Zygapophyses - In most neotheropod clades, such as abelisauroids (e.g., O'Connor, 2007, but see Novas *et al.*, 2004), basal tetanurans (Madsen, 1976; Allain & Chure, 2002), basal coelurosaurs (Carpenter *et al.*, 2005) including tyrannosaurids (Brochu, 2003), ornithomimosaurids (Kobayashi, 2004), and dromaeosaurids

(Ostrom, 1969; Kirkland *et al.*, 1993; Norell & Makovichy, 1999), those prezygapophyses that occur distal to the transition point are very prominent and elongate, and reduce only in the distal-most vertebrae where the neural spine is completely absent. MSNM V6408 shows the opposite condition: the neural spine is short and low but robust, while the zygapophyses are reduced.

By analogy with the position of the transition point, the position of the first caudal bearing coalesced postzygapophyses varies among theropods, showing a trend toward a more proximal position in more bird-like theropods: in the non-tetanurans *Elaphrosaurus* and *Coelophysis* the fusion of the postzygapophyses occurs in the distal-most caudal vertebrae (Janensch, 1925; Colbert, 1989); in the non-coelurosaurian tetanuran *Allosaurus* it occurs distal to the 48th caudal (Madsen, 1976); in the basal coelurosaur *Tyrannosaurus*, distal to the 32th position (Brochu, 2003); in the maniraptoriform *Harpymimus* it occurs at the level of the 22nd caudal (Kobayashi, 2004); in the dromaeosaurid maniraptoran *Velociraptor*, it occurs distal to the 24th caudal (Norell & Makovichy, 1999); and in the oviraptorosaurian maniraptorans IGM 100/42 and *Nomingia* it occurs, respectively, at the 16th and 14th caudal (Audatore, pers. comm., 2008; Barsbold *et al.*, 2000). Interestingly, the condition among abelisauroids is more variable: in some forms the coalescence of the postzygapophyses occurs in the distal caudals, after the reduction or loss of both neural spines and transverse processes (*Majungasaurus* O'Connor, 2007; *Masiakasaurus*, Carrano *et al.*, 2002), whereas in others it occurs in the middle caudals (*Ilokelesia*, Coria & Salgado, 2000; *Ligabueino*, Bonaparte, 1996). The Moroccan specimen is similar to *Ilokelesia* in that a robust neural spine is present in the same part of the tail as are coalesced postzygapophyses. Compared with the reduction of the neural spines, we hypothesise that the coalescence of postzygapophyses in the tail of *Kemkemia* started in a more proximal position compared to the tails of, for example, *Majungasaurus*, *Masiakasaurus*, *Allosaurus*, *Tyrannosaurus* and *Harpymimus*.

MSNM 6408 differs from coelophysid distal caudals in the relatively less elongate centra and in the presence of spinal laminae (Wilson *et al.*, 2003, Appendix), and from *Dilophosaurus* and several basal (non-coelurosaurian) tetanurans in the shape and robustness of the neural spine and in the relatively less elongate prezygapophyses (Madsen, 1976; Rauhut, 2003; Welles, 1984). It differs from the distal caudals of most coelurosaurs in the presence of a robust neural spine (Brochu, 2003; Currie & Chen, 2001; Kobayashi, 2004; Ostrom, 1969), and from oviraptorosaurs in the relatively narrower and more elongate centrum (Makovicky & Sues, 1998; Barsbold *et al.*, 2000). Among known theropod middle and distal caudals, the combination of features observed in MSNM V6408 resembles that of some ceratosaur middle and distal caudals: namely, the caudal vertebrae have transversely wide neural spines (Coria & Salgado, 2000: fig. 9A; Madsen & Welles, 2000; Novas *et al.*, 2004; O'Connor, 2007), and possess distinct neural spines and coalesced postzygapophyses (Bonaparte, 1996; Coria & Salgado, 2000). However, we note that *Kemkemia* differs markedly from the distal caudals of the only two abelisauroids where such elements are well described (i.e., *Masiakasaurus* and *Majungasaurus*, Carrano *et al.*, 2002; O'Connor, 2007) in the development of both a neural spine and prezygapophyses. Novas *et al.* (2004) reported two morphologies of distal caudal vertebrae in the theropod material from the Lameta Formation (Maastrichtian) of India (Huene & Matley, 1933). Both morphologies share similar elongation, but differ in the development of the vertebral processes: the

first, including caudals that bear elongate prezygapophyses and well developed “alariform” transverse processes, resembles *Masiakasaurus* (Novas *et al.*, 2004: 87) and *Majungasaurus* (O’Connor, 2007); the second, with robust neural spines, very short prezygapophyses and nearly absent transverse processes (Novas *et al.*, 2004; fig. 22), is very similar to *Kemkemia*. We note that one of these specimens (GSI K27-599, Huene & Matley, 1933, Plate XXIII, Fig.4) shows a morphology intermediate between MSNM V6408 and that seen in the abelisauroids *Ligabueino* and *Masiakasaurus*: hypertrophied neural canals are present, as are peculiar alariform transverse processes with dorsal excavations (Novas *et al.*, 2004). Compared with the Indian caudals, MSNM V6408 is relatively more elongate and narrow, and shows narrower and more reduced prezygapophyses, a taller neural arch and a neural spine that is relatively more prominent and robust. Whereas the former two features may indicate that the Moroccan specimen was positioned more distally along the tail than were the Indian ones, the prezygapophyseal and neural spine characters are interpreted as autapomorphic conditions useful in distinguishing *Kemkemia* from the Lameta forms. These data suggest the existence of a previously unknown lineage of theropods differing from other taxa in the presence of elongate distal caudals bearing transversely robust neural spines and very reduced prezygapophyses.

In conclusion, although the presence of some derived features suggests that MSNM V6408 may belong to the ceratosaurian lineage, we provisionally refer *Kemkemia auditorei* to Neotheropoda *incertae sedis*, pending the discovery of more complete material.

Comparison between *Kemkemia* and the theropod fossil record from the Kem Kem Beds - Based on comparison with several neotheropods (Gilmore, 1920; Janensch, 1925; Madsen, 1976; Welles, 1984; O’Connor, 2007), we estimate that the body size of *Kemkemia* was comparable to that of *Dilophosaurus* and *Elaphrosaurus* (Fig. 4). Although three theropod genera have been found in the Kem Kem Beds - *Carcharodontosaurus*, *Spinosaurus* and *Deltadromeus* (Russell, 1996; Sereno *et al.*, 1996) - only the distal caudal vertebrae of the latter are known. Following Novas *et al.* (2005), we do not consider *Sigilmassasaurus* (Russell, 1996) a junior synonym of *Carcharodontosaurus* (but see Sereno *et al.*, 1996; and Brusatte & Sereno, 2007; for a different interpretation of their synonymy). Our conclusion is based on two evidences: 1) Russell (1996) referred a partial cervical vertebra, NMC 50792, to *Carcharodontosaurus*, noting its similarities with a cervical vertebra referred by Stromer to the latter genus (Stromer, 1931: 11-12, pl. I, fig. 9). We concur with that identification, noting that NMC 50792 shares three carcharodontosaurid apomorphies: a hyposphene-like process ventral to the postzygapophyses (Russell, 1996: fig. 16b; Coria & Currie, 2006); a pneumatic fossa bearing multiple foramina on centrum (Russell, 1996: fig. 16c; Harris, 1998; Brusatte & Sereno, 2008); and a pair of large peduncular fossae between the neural canal and the prezygapophyses (Russell, 1996: fig. 16d; Harris, 1998; Novas *et al.*, 2005b). 2) The holotypic and referred cervical vertebrae of *Sigilmassasaurus* (Russell, 1996) lack the character conditions cited above, retaining the non-carcharodontosaurid plesiomorphies (single pleurocoelic fossa lacking multiple foramina; absence of hyposphene-like process; absence of peduncular fossae). If the presacral vertebrae of the “*Sigilmassasaurus* morphotype” would belong to *Carcharodontosaurus* (Sereno *et al.*, 1996; Brusatte & Sereno, 2007), then NMC 50792, from the same beds, should be referred to a new and distinct theropod, clearly belonging to the

carcharodontosaurid lineage. Based on cranial and dental data, there is no evidence that more than one carcharodontosaurid species co-occurred in the Kem Kem Beds (Brusatte & Sereno, 2007), nor in other Cretaceous North African localities (Sereno & Brusatte, 2008). Therefore, given that the “*Sigilmassasaurus* morphotype” lacks many of the carcharodontosaurid features present in NMC 50792, the most parsimonious explanation of the evidence is to refer the latter to *Carcharodontosaurus saharicus*, and to consider *Sigilmassasaurus brevicollis* a distinct species of dinosaur. Regardless to the taxonomic status of *Sigilmassasaurus*, its referred distal caudal vertebrae from the Kem Kem Beds (Russell, 1998) are clearly distinct from MSNM V6408 in shape and elongation of both centrum and postzygapophyses.

No distal caudal vertebrae of *Spinosaurus* and *Carcharodontosaurus* are known up to today. We cannot completely dismiss the hypothesis that MSNM V6408 belongs to one of these tetanurans. Nevertheless, based on comparison with their closest relatives, the most parsimonious hypothesis is that the distal caudals of these theropods should be similar to those of other basal tetanurans (Madsen, 1976; Allain & Chure, 2002; Coria & Currie, 2006) and, as a consequence, should be clearly different from MSNM V6408. We note that all known tetanurans share marked reduction of the neural spines on the distal caudals (Madsen, 1976; Allain & Chure, 2002; Brochu, 2003; Coria & Currie, 2006): as stated above, the most parsimonious interpretation is to consider *Kemkemia* a non-tetanuran neotheropod.

Deltadromeus is a large-bodied theropod from the same stratigraphic beds as *Kemkemia* (Sereno *et al.*, 1996). Initially referred to Coelurosauria (Sereno *et al.*, 1996; Rauhut, 2003), it is now considered to be a ceratosaur (Sereno *et al.*, 2004; Carrano & Sampson, 2008). Regardless of the phylogenetic position of *Deltadromeus*, its distal caudals differ from those of *Kemkemia* in lacking the marked



Fig. 4 - Estimated size of *Kemkemia* gen. nov. compared with *Homo* (1.74 m tall) and the largest known individuals of some of the other theropod genera recovered from the Kem Kem Beds: from left to right, *Spinosaurus* (based on Dal Sasso *et al.*, 2005), *Carcharodontosaurus* (Sereno *et al.*, 1996; modified from a drawing by Marco Auditore), *Deltadromeus* (modified from Sereno *et al.*, 1996), *Kemkemia* (this study; silhouette based on several basal neotheropods). (Drawing by AC).

Fig. 4 - Taglia stimata di *Kemkemia* gen. nov. comparata con *Homo* (altezza 1,74 m) e con gli individui più grandi di alcuni degli altri generi di teropodi rinvenuti nei letti del Kem Kem: da sinistra a destra, *Spinosaurus* (basato su Dal Sasso *et al.*, 2005), *Carcharodontosaurus* (Sereno *et al.*, 1996, modificato da un disegno di Marco Auditore), *Deltadromeus* (modificato da Sereno *et al.*, 1996) e *Kemkemia* (questo studio, sagoma basata su alcuni neoteropodi basali). (Disegno di AC).

mediolateral compression of the latter (in *Deltadromeus* the minimum diameter of the vertebra is 27% of vertebral length, whereas in *Kemkemia* it is 13%, Sereno *et al.*, 1996, Table 1), and in having more prominent prezygapophyses that overlap at least 40% of the preceding centrum (Wilson *et al.*, 2003, Appendix).

Among the other theropod remains from the Cenomanian of Morocco, two caudal vertebrae from Tafilalt have also been reported (NMC 41863 and NMC 50797, “Bone Taxon B” of Russell, 1996: 378). They differ from MSNM V6408 in the stronger development of their zygapophyseal bases, in the shape of the neural spine, and in the presence of a relatively narrower neural canal.

In recent years, some isolated theropod remains from the Kem Kem Beds have been referred to Abelisauridae (Russell, 1996; Mahler, 2005; Carrano & Sampson, 2008). UCPC 10 is a maxillary fragment found in the Kem Kem Beds (Mahler, 2005). It exhibits several abelisaurid apomorphies, including a textured lateral surface, *lamina lateralis* and *medialis* of subequal depth, deep fused paradental laminae, and subrectangular alveoli (Sereno *et al.*, 2004; Carrano & Sampson, 2008), but appears less derived than the maxillae of most abelisaurids in having faint shallow striations along the medial surface of the paradental plates instead of more furrowed plates (Carrano & Sampson, 2008). Nevertheless, as observed in carcharodontosaurids (Coria & Currie, 2006), the development of both lateral striations and medial paradental furrows may be ontogenetically controlled, so UCPC 10 may not have been fully grown at the time of death. Given that most of these features occurs homoplastically in derived carcharodontosaurids (Brusatte & Sereno, 2007), some authors have questioned the abelisaurid affinities of UCPC 10 (Carrano & Sampson, 2008). Nevertheless, this specimen shows further abelisaurid features (Sereno & Brusatte, 2008): a subvertical rostral end of the rostral ramus, a rostro-medially directed premaxillary facet, and a row of foramina located immediately above the alveolar border. Furthermore, it differs from carcharodontosaurid maxillae as these possess a caudodorsally inclined rostral ramus, a rostrally directed premaxillary facet, and a row of ventral foramina that are located more dorsally (Brusatte & Sereno, 2008). We therefore support Mahler’s (2005) interpretation and regard UCPC 10 as an abelisaurid maxilla. Based on comparison with *Majungasaurus* (Sampson & Krause, 2007), we estimate that UCPC 10 belonged to an individual about 5.5 meters long.

NMC 50807 and NMC 50808 are two skull roof fragments from Tafilalt (Russell, 1996). Although Russell (1996) considered them “Theropoda indet.”, Carrano & Sampson (2008) noted that they show neoceratosaurian apomorphies, including frontals that are fused and bear a sloped and striated nasal contact, and a sagittal parietal crest between the supratemporal fenestrae. We also note that NMC 50808 lacks an extensive ossification of the interorbital region (Russell, 1996: fig. 18), a derived feature shared by *Ceratosaurus* and abelisaurids (Carrano & Sampson, 2008: 224). These data may indicate that NMC 50807 and NMC 50808 belong to a basal (non-abelisaurid) neoceratosaur such as *Deltadromeus* (following the phylogenetic interpretation of that taxon favoured by Carrano & Sampson, 2008).

NMC 41589 and NMC 41861 are two fragmentary dentary rami from Tafilalt (Russell, 1996). They have been referred to Abelisauridae on the basis of the massively constructed lateral surface marked with indistinct vertical ridges, a marked craniomedial curvature of the alveolar margin, subrectangular alveoli, and fused paradental laminae. Although these features have a broader distribution among Theropoda (Carrano & Sampson, 2008), being also present in carcharodontosau-

rids (Brusatte & Sereno, 2008), we note that NMC 41589 shares with the abelisaurids *Carnotaurus*, *Majungasaurus* and *Ekrixinatosaurus* the presence of the lateral groove on the bone's ventral half (Carrano & Sampson, 2008: 226). Based on comparison with *Majungasaurus* (Sampson & Krause, 2007), we estimate that NMC 41589 belonged to a individual about 7-9 meters long.

These data indicate that at least one abelisaurid species is present in the Kem Kem Beds. While we note some resemblance between MSNM V6408 and the mid- and distal caudals of some abelisauroid taxa (see above), we cannot unambiguously refer any of the abelisaurid specimens from the Kem Kem Beds to *Kemkemia*.

We propose that more than three genera of middle- to large-sized theropods lived sympatrically in the Cenomanian of Morocco: the spinosauroid *Spinosaurus*, the allosauroid *Carcharodontosaurus*, the non-abelisaurid ceratosaur *Deltadromeus*, *Kemkemia* and (if further evidence will support the taxonomic distinction from *Kemkemia*) a yet-unnamed abelisaurid. The high diversity of middle- to large-sized carnivorous dinosaurs in the Kem Kem Beds recalls that found in other Mesozoic formations (e.g., the Morrison Formation, Weishampel *et al.*, 2004; or the Wealdien Supergroup, Brusatte *et al.*, 2008). Nevertheless, it is unusual in contrasting with the relatively lower diversity of local herbivores (Russell, 1996; Sereno *et al.*, 1996; Mahler, 2005) and may indicate either that there is a high under-sampling of local herbivores or the evolution of some intense form of competition and/or niche partitioning among the carnivores (Holtz, pers. com., 2008). Large fish are extremely abundant in the Kem Kem Beds (Sereno *et al.*, 1996; Naish, pers. comm., 2009). It is possible that this resource helps explain the diversity and number of predatory dinosaurs in the assemblage. By virtue of their simple digestive system and adaptability, carnivorous taxa can survive in poor environments where resources are few and far between. A similar phenomenon occurs in the Santana Formation of Brazil, where several theropod taxa are known, but no ornithischians or sauropodomorphs (Naish *et al.*, 2004).

Functional implications - In MSNM V6408, the presence of strongly reduced zygapophyses lacking articular surfaces shows that the intervertebral movement along the tail of *Kemkemia* was relatively more extensive than that of most theropods, whose tails are stiffened by overlapping zygapophyses. The presence of robust neural spines bearing pre- and postspinal laminae probably indicates that the epaxial musculature and interspinal ligaments compensated for the absence of zygapophyseal articulation between the neural arches. In particular, the concave dorsal surface of the neural spine may imply the presence of a continuous ligament linking the caudal vertebrae that helped in raising the tail following ventroflexion (Wedel *et al.*, 2000).

Conclusions

While based only on a single vertebra, *Kemkemia audirei* shows a unique and unusual combination of features that distinguishes it from all other saurischian caudal vertebrae. Other saurischian species have been diagnosed on the basis of very fragmentary vertebral specimens (e.g., Carvalho *et al.*, 2003) if not on single vertebrae (e.g., Apesteguía, 2007; Taylor & Naish, 2007), or have been suggested on the basis of isolated bones (Longrich, 2008). Interestingly, other fossil taxa based on remains more complete than MSNM V6408 have been defined on a comparable list of vertebral diagnostic features (e.g., *Spinostropheus gautieri* Sereno

et al., 2004; and *Lophostropheus airelensis* Ezcurra & Cuny, 2007). Some authors have been reluctant to name new species on the basis of very fragmentary remains, noting that these specimens may be unique when first found, but later shown to be indeterminate as further discoveries reveal their distinctive features to characterize a clade rather than a single species (Longrich, 2008). Wilson & Upchurch (2003) termed this phenomenon “character obsolescence”. We note that this phenomenon is not unique to fragmentary remains: it is instead a feature of almost all palaeontological species given that they are defined on the basis of a list of autapomorphic characters whose taxonomic distribution broadens once new relevant discoveries are made (Sues, 1998). As noted elsewhere (Taylor & Naish, 2007), the number of recognizable autapomorphies is the most valid criterion for the erection of a new taxonomic name. In our opinion, the naming of autapomorphy-bearing taxa is important - even when the remains are extremely fragmentary - because named taxa get noticed by the community at large, whereas unnamed ones - even if noted by authors as representing possible or potential new taxa - do not. We concur with Naish & Martill (2007) that “naming taxa, even those based on fragmentary remains, can be a useful exercise simply because named taxa are incorporated into large-scale studies of systematics and diversity. Unnamed taxa, even those thought to represent new species, generally are not” (Naish & Martill 2007: 506). MSNM V6408 is unique among theropod distal caudal vertebrae in both its presence of autapomorphic conditions (inflated neural canal, strongly reduced prezygapophyses, very broad neural spine, presence of shallow spinal fossae and transversely concave dorsal surface of the neural spine), and its unusual combination of features (simultaneous presence of reduced zygapophyses and robust neural spine bearing pre- and postspinal laminae). Following Taylor & Naish (2007)’s criterion, *Kemkemia auditorei* is clearly distinct from other theropods and worthy of consideration as a valid taxon.

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